

Life-History Patterns in the Elasmobranchs: Implications for Fisheries Management

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ABSTRACT

The life-history patterns of elasmobranchs are very different from most teleosts and appear to fall in the realm of the so-called "K-selected species" of classic r/K selection theory. The authors explore the connections between life-history studies, r/K selection theory, and the theory of fisheries management. Considerations of life history and the predictions of r/K selection theory can provide useful results for fisheries management in two ways: by providing estimates of, and methods for estimating, important life-history parameters and by providing a basis for predicting and ranking the resiliency of species to exploitation. The rate of population increase appears implicitly in stock production models and age-structured (e.g., Leslie matrix) models of fisheries management. Considerations of life history patterns may provide guidance in quantifying the intrinsic rate of increase.

Introduction

Elasmobranchs have been evolving independently for at least 450 million years and, by the Carboniferous period, they seem to have developed a life-history pattern similar to that seen today. This pattern, typically consisting of slow growth, large adult size, late reproduction, and the production of few, well-formed young, is quite different from that typically found in the other great class of fish-like vertebrates, the teleosts. Here the pattern generally seen consists of rapid growth, a relatively short life cycle, and many fragile offspring. Elasmobranchs in essence have evolved a life-history strategy very similar to the marine reptiles and mammals.

Most traditional fishery models developed for teleosts do not assume any direct relationship between stock and

recruitment (Ricker 1975), although such a relationship must exist because no fish present implies no recruitment. Highly variable survival of the early life stages of teleosts has long been noted, and environmental conditions during the first year of life appear to play an important role in determining the recruitment of new cohorts into teleost stocks (Rothschild 1986). On the other hand, the relationship between stock and recruitment in the elasmobranchs is quite direct, owing to the reproductive strategy of low fecundity combined with few, well-formed offspring. Although there is some evidence that fecundity of sharks increases as the stocks decline (Holden 1977), in general the number of young that can be produced is strictly limited and dependent on the number of adults in the stock. Thus, unlike the strategy for a cod or flounder fishery, the relationship between parental stock and recruitment success must be of prime consideration in the development of a rational strategy for exploitation of elasmobranch stocks.

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From a practical point of view the life-history pattern of elasmobranchs makes this group of animals extremely susceptible to over fishing. It is no coincidence that the commercially exploited marine turtles and baleen whales, which have life-history patterns similar to the sharks, are also in trouble. Indeed, the strong relationship between parental stock and recruitment in the elasmobranchs has led some to question whether it is possible to have sustained exploitation (Holden 1974). If this question is taken literally, the answer is obviously "yes"—many wild animals, such as the ungulates, have life-history traits similar to those mentioned for the elasmobranchs yet they have supported sustained harvests for centuries. On a deeper level, it is less clear whether effective management strategies can (will) be developed to deal with the specific problems associated with elasmobranch life-history patterns and the structure of elasmobranch fisheries. Factors such as bycatch, difficulty in obtaining accurate landing statistics due to the diffuse nature of the fish handling systems, low priorities assigned by management agencies due to low values of the landings, etc. make it difficult to develop and implement effective management measures.

How can fisheries scientists provide advice on the management of elasmobranch stocks given the above limitations? Intensive and extensive study of more than a few stocks does not appear to be a viable option. Therefore, we need to look at life-history patterns and processes in a more generic sense. Can we identify aspects of life history that appear to be strongly related to the ability of a species to withstand exploitation? Can we identify conditions that are useful indicators of overexploitation? If so, then we have a good chance of developing useful tools for planning and management.

Because of the importance of life-history pattern to fisheries management, it seems appropriate to begin this article with a consideration of just what "life-history pattern" means, how it is studied, and what it can tell us. We discuss the relevance of r/K selection theory to elasmobranch life-history studies and show how this paradigm provides guidance for estimating parameters needed for fisheries assessment and management.

Life-History Pattern and Strategy _____

Biologists frequently describe a species by a process akin to looking at a series of static 'snapshots' of the species in time. Description is based on a series of specimens of different sizes or ages. Such an account of the biology can be used to describe the "life-history pattern" of the species which, in the view of Horn (1978), implies the organism's lifetime pattern of growth, differentiation, storage, and especially reproduction. In our view, a more enlightening definition involves looking at the organisms in terms of their responses to environmental conditions. The life-history

pattern of a species or a stock can be defined as the characteristic set of biological episodes and responses occurring during the lifetimes of the individuals in the population. These responses or episodes include where and when the animals are born, how long they remain there, how fast they grow, what and how much they eat, their social and sexual relationships, when and where and how often they mate, how many young are produced, their movements and migrations, and so on. Such definitions emphasize descriptive aspects of the morphology, physiology, and ecology of the species. The latter definition makes clear the plastic nature of life-history pattern by emphasizing the connection between environmental conditions and biological response. Inasmuch as environmental conditions vary from location to location and from year to year, the definition provides for variability in life-history traits both among individuals and among stocks within a species. And, inasmuch as environmental conditions vary over geological time, the latter definition also provides a link between life-history pattern and evolutionary trends.

Given a description of the life-history pattern of a species or a population, it is natural to ask why the animals have these particular traits or how this collection of traits arose. This leads to the idea of life-history strategy which Stearns (1976) describes as a research concept that combines the study of reproduction, growth, and genetics in an ecological setting to produce hypotheses concerning evolutionary changes. Here "strategy" is thought of as a set of traits brought about by natural selection to solve particular ecological problems. Simply put: in the game of life, an animal stakes its offspring against a capricious and unreliable environment. The animal wins the game if its offspring live to play another round. The appropriate tactics (pattern) for winning the game comprise the successful life-history strategy.

Life Histories in the Elasmobranchs _____

Any characteristic which affects the survival and reproduction of an animal is, by definition, a part of the life-history pattern of the species. This means there are an unlimited number of variables to observe and measure. Since this is obviously impossible, life-history studies necessarily concentrate on those aspects of the life history that seem most relevant to the research question of interest. Observations are generally made on composite variables or integrated responses, that is, on aspects of the life history which are, in themselves, the results of many other responses to environmental conditions. Some of the most reported aspects of life history are described below as they apply to the elasmobranchs.

Maximum Size—This is perhaps the most obvious character to study because it is easy to measure and tends

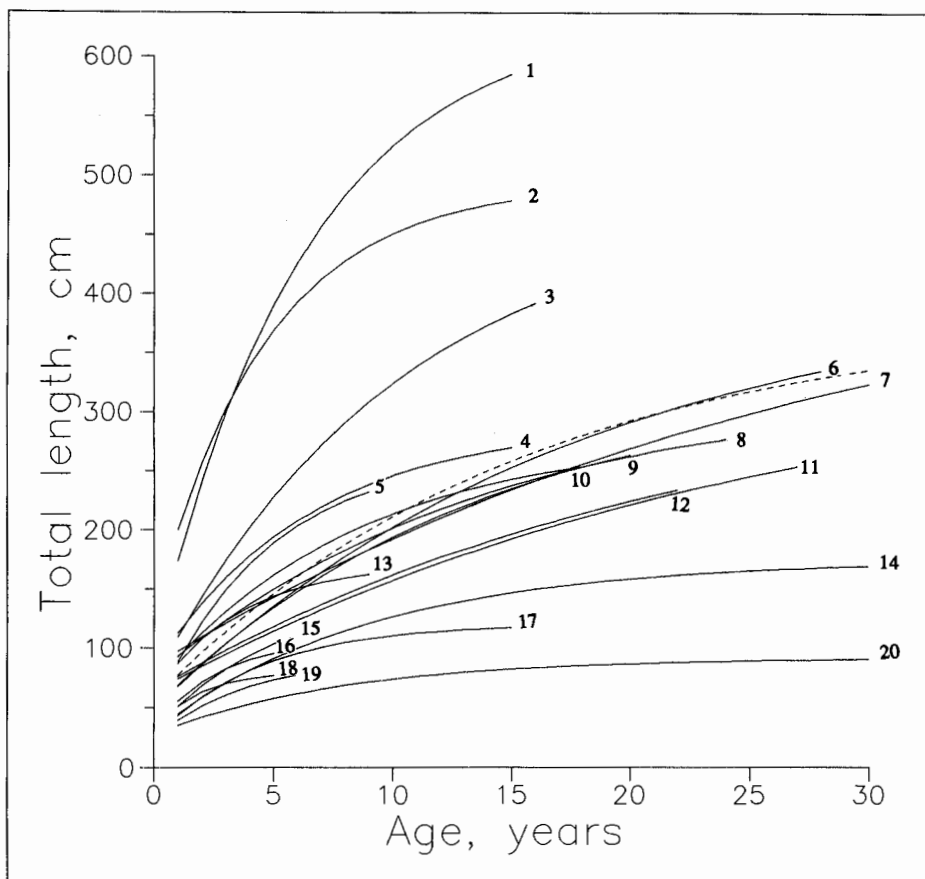


Figure 1.

Growth rates of sharks (solid lines) and of bluefin tuna (dashed line) (based on Hoenig 1979 and Brown 1988). Longevities shown are approximate, except that growth curves for *Squalus acanthias* and *Galeorhinus australis* are truncated at 30 years. Key to sharks: 1) *Alopias vulpinus* (female); 2) *Alopias vulpinus* (male); 3) *Galeorcerdo cuvieri*; 4) *Carcharhinus falciformis*; 5) *Prionace glauca*; 6) *Negaprion brevirostris*; 7) *Carcharhinus obscurus*; 8) *Isurus oxyrinchus*; 9) *Sphyrna lewini*; 10) *Lamna nasus*; 11) *Carcharhinus leucus*; 12) *Carcharhinus plumbeus*; 13) *Carcharhinus limbatus*; 14) *Galeorhinus australis*; 15) *Mustelus californicus*; 16) *Rhizoprionodon terraenovae*; 17) *Galeorhinus japonicus*; 18) *Mustelus manzo*; 19) *Mustelus henlei*; 20) *Squalus acanthias*.

to be strongly related to a number of important processes such as consumption, mortality rate, and intrinsic rate of population increase (Blueweiss et al. 1978). The largest shark is the whale shark, *Rhincodon typus*, which reaches perhaps 2000 cm in length; the smallest squaloids and proscyllids reach maximum sizes a little above 20 cm. The largest shark is thus some two orders of magnitude longer than the smallest. This large range of sizes suggests that there should be interesting variability in other life-history parameters and processes within the elasmobranchs.

Most commercially utilized sharks are near the small end of the spectrum, measuring roughly a meter or two at full size (e.g., *Squalus acanthias*, *Mustelus* spp., *Galeorhinus* spp., *Scyliorhinus* spp.). However, the large sharks are actively sought by sport fishermen and are captured as bycatch in longline and other fisheries. Most of the commercially utilized skates and rays are under a meter in size (disc width).

Sexual Dimorphism in Size—Among the carcharhinid sharks, it is commonly observed that females grow to a larger size than males (Bigelow and Schroeder 1948). In other groups, sexual dimorphism in size may be absent or not very pronounced.

Individual Rates of Growth—Growth, the increase in somatic tissue over time, gives rise to the organism's final

size and is obviously a major determinant of potential yield. Traditionally, elasmobranchs have been considered slow growing animals but this view has been subject to some misunderstanding. As in most other fishes, the rate of growth of a shark (in cm/yr) decreases continually as the shark ages (Fig. 1). Thus, a single parameter is insufficient to describe the growth rate of a species. Porbeagles, *Lamna nasus*, grow faster than dusky sharks, *Carcharhinus obscurus*, at early ages but by age 17 both species are the same size (roughly 250 cm total length). At ages greater than about 10 years, the annual growth of dusky sharks is greater than that of porbeagles. Which species "grows faster" is not readily apparent. In terms of total increase in length or weight per unit of time, a shark at almost any age will increase in size faster than a stickleback (*Gasterosteus* spp.), because sticklebacks attain such a small size. Perhaps more to the point, the growth curve for bluefin tuna, *Thunnus thynnus*, an extremely important commercial species, does not suggest faster growth than is found in a number of sharks (Fig. 1).

It is certainly true that the rate at which shark growth slows down with age tends to be very slow. The usual descriptor of fish growth is the familiar von Bertalanffy growth function

$$L_t = L_\infty(1 - e^{-k(t-t_0)}), \quad (1)$$

where L_t is the length at age t , L_∞ is the asymptotic or ultimate length, k is the growth coefficient determining the degree of curvature or rate at which growth slows, and t_0 is a location parameter. Sharks tend to have among the lowest values of k of any fishes.

Finally, if we consider the amount of growth occurring in a shark population, averaged over the individuals in the population, then growth may be considered quite slow. This is because sharks tend to have low natural mortality and high longevity so that there are many old, slow growing individuals in the population. Thus, the production in a shark population tends to be low.

Energetics—Energetics refers to the amount of energy obtained from food by an animal, the efficiency with which this energy is assimilated, and the allocation of the energy to maintenance, growth, reproduction, and other life processes. Energetic relationships are dynamic and depend on the age or size of the animal, the environmental conditions (temperature, etc.) and the quality and quantity of the available food. Some elasmobranchs are sluggish; some capture prey by active pursuit or by ambushing passing animals. Many sharks are extremely active and some have even evolved the ability to maintain elevated body temperatures and to regulate body temperature to varying degrees (Carey et al. 1971). In general, little is known about energetic requirements and relationships in the elasmobranchs (Gruber 1984; Medved et al. 1988; Wetherbee et al. 1990) In their review of shark energetics, Wetherbee et al. found the following:

- food appears to pass through the alimentary tract of sharks more slowly than in teleosts; from the literature, estimates of the time required for a meal to be completely removed from the stomach range from 24 to 124 hours for five species of shark.
- the lemon shark, *N. brevirostris*, was observed to absorb energy from a meal with an efficiency comparable to that of most teleosts.
- estimates of daily ration for sharks are lower than for most teleosts; estimates for four species of shark range from 0.4 to 3.2% of body weight per day.

Only a few attempts have been made to estimate the annual consumption of prey by a shark population (Medved et al. 1988) and these estimates, in our opinion, are extremely rough.

Development—Development is the progressive differentiation of an organism. All of the elasmobranchs are born or hatched in a well-developed state. A few species of sharks, and many skates and rays, may attain sexual maturity within two years. But the majority of large sharks are slow to mature (Pratt and Casey 1990). Little is known about the control of onset of sexual maturity in sharks (Wourms et al. 1988). An important question is to what

degree can development be speeded up by changing environmental conditions.

Reproduction—Tremendous variation is seen in the reproductive patterns in elasmobranchs including viviparity, oviparity and ovoviviparity, and even some unusual variations such as oviphagous (egg-eating) embryos. Detailed surveys of the modes of reproduction in the Chondrichthyes are presented by Wourms (1977), Wourms et al. (1988), and Otake (1990).

Despite the variation in observed pattern, a few features appear to be common to most, if not all, members of the group. All are iteroparous (reproducing more than once) rather than semelparous (producing all their young at one time). All produce young that are well-developed compared to the fragile early life stages of teleosts. All have severely limited numbers of young. Large blue sharks, *Prionace glauca*, and tiger sharks, *Galeocerdo cuvieri*, may produce more than 80 young at one time (Pratt 1979; Bigelow and Schroeder 1948), but most sharks produce far fewer. The bigeye thresher, *Alopias superciliosus*, produces two embryos at a time (Gruber and Compagno 1981). Female sharks produce young once or twice a year or every other year. Skates and rays also produce small numbers of young at a time but may continue to produce them throughout most of the year.

Parental Care—Sharks do not receive parental care as far as we know.

Mating Systems—There is no evidence that elasmobranchs have developed the wide variety of mating systems, such as long term pairing, polygyny, polyandry, and promiscuity, seen in birds and mammals. However, copulation has been observed in only a very few species (Clark 1963; Clark and von Schmidt 1965; Uchida 1990) and virtually nothing is known about social organization and possible mating systems. Tooth cuts on females in some species are perhaps indirect evidence of courtship activity (Stevens 1974; Pratt 1979).

Dispersal and Migration—Movements of sharks are an important aspect of life history inasmuch as they affect survival. We have much to learn about shark movements, but what we do know indicates that there is considerable variability among species. The movements of juvenile lemon sharks, *N. brevirostris*, appear to be extremely restricted (generally less than a mile) during the first several years of life (Gruber et al. 1988). Young sandbar sharks, *Carcharhinus plumbeus*, appear to be restricted to shallow areas during the warm part of the year but move to unknown locations in the winter (Springer 1960; Musick 1986). Tagging of adult sharks has shown that some species undertake spectacular long-distance movements including trans-Atlantic and trans-Pacific movements and movements

between South America and the Canadian Atlantic (Olsen 1954; Holland 1957; Holden 1967; Stevens 1975; Templeman 1976; Casey et al. 1978). Only short-distance movements have been noted in other tagging studies. Interestingly, long-distance movements have been reported for some small species, notably the spiny dogfish, *S. acanthias*, and the school shark, *Galeorhinus australis*.

Social Segregation—It is commonly observed that catches of sharks have a preponderance of one sex or the other, or are composed of animals of a limited size range. Evidently, many species segregate by size and by sex (Pratt 1979). This type of segregation can be based on habitat, i.e., be local in nature, or occur on a wide geographical scale.

Storage of Energy—Sharks have large livers which store high-energy, fatty acids. Apparently, these lipids serve not only to provide buoyancy but also to provide stored resources for use during hard times (Oguri 1990). We believe a large liver is an adaptive character for predators that live under feast-or-famine regimes.

Longevity—Sharks are among the longest lived fishes. Based on vertebral rings or rings in dorsal spines, the following ages have been reported: for *S. acanthias*, 65–70 years (Ketchen 1975; Jones and Geen 1977); for the bull shark, *Carcharhinus leucas*, 27 years (Hoenig 1979); for the dusky shark, *C. obscurus*, 30 years (Hoenig 1979); for lemon sharks, *N. brevirostris*, 21 years (Brown and Gruber 1988). A school shark, *G. australis*, estimated to be at least 18 years old at the time of tagging was recaptured 25 years later, thus yielding an estimated age of 43 years (Anon. 1976). Grant et al. (1979) reported the recapture of six tagged school sharks that had remained at liberty from 23 years to 27 years and 8 months. The longevity of batoid fishes can also be high. Martin and Cailliet (1988) reported a maximum age of 23 years for female bat rays, *Myliobatis californica*, based on vertebral rings.

It is curious that the oldest ages reported for sharks are from two small species. High longevity is usually associated with large adult body size (Blueweiss et al. 1978). It should be noted that workers have had a great deal of difficulty procuring vertebral samples from large specimens, and methods for elucidating growth bands are still being developed; hence, the oldest ages may have been missed altogether.

Natural Mortality—Natural mortality differs from the other parameters considered so far in that it is a property of populations, not individuals. You cannot measure how fast an individual dies, because an individual can only be either alive or dead. Fishery scientists often estimate mortality rates from the age composition of a sample, but this is difficult for many shark species because the pattern of segregation by age makes it difficult to obtain an unbiased

sample. Also, until the work of Stevens (1975), it was generally not considered possible to age sharks from vertebral rings. There are only a few direct estimates of natural mortality for sharks, notably: for the school shark, *G. australis*, 13% per year annual (finite) rate (Grant et al. 1979); for the porbeagle, *L. nasus*, 16% (Aasen 1963); for the spiny dogfish, *S. acanthias*, 9% (Wood et al. 1979). Natural mortality of adult little skate, *Raja erinacea*, was estimated to be 33% (Johnson 1979). The paucity of information on mortality led Hoenig (1983) to suggest using the relationship between longevity and mortality to estimate mortality rates.

Intrinsic Rate of Population Increase, r —This is another property of populations rather than of individuals. We defer a formal definition to the section on r/K selection theory and note here that this parameter describes the innate or intrinsic ability of a population to increase in size when confronted with favorable environmental conditions. For example, if the size of a population is reduced by temporary fishing, then crowding and competition for resources should be reduced. This should result in an opportunity for the population to grow back to its former size once fishing is reduced. The parameter r is a composite of many factors which determine population growth through three mechanisms:

- changes in individual body growth rates
- changes in natural mortality
- changes in reproduction.

Intrinsic rate of increase has been studied in the laboratory for a few species only, mostly micro-organisms and insects. Observations on population increase in the wild are even more scarce. However, one can calculate this quantity from some types of commercial fisheries data, such as from the parameters of a Schaefer (1957) stock production model. Life table, Leslie matrix, and other “book keeping” types of models can be used to estimate “observed rate of increase”, which may be considered a minimal estimate of intrinsic rate of population increase.

No estimates of intrinsic rate of population increase are available for elasmobranchs. However, as we shall see, there are some indirect methods appropriate for estimating this quantity.

What Do Life-History Studies Tell Us? —

Clearly, many of the parameters estimated in a study of life history, such as growth and mortality rates, have immediate management value as input to assessment models. Even when insufficient information has been collected to conduct a complete assessment of a stock, the available information may still provide valuable guidance. For example, if a comparative study shows two parameters such as

natural mortality and longevity to be closely related (Tanaka 1960; Hoenig 1983; Hoenig et al. 1987), then the information on one parameter may be used to estimate the value of the other from a regression relationship. Even if the available information is inadequate to develop estimates of all parameters needed for assessment models, it may still be possible to make qualitative statements about the need for regulation based on the "assessment by analogy" concept (Hoenig et al. 1987). Thus, one might speculate that if conditions in a fishery of interest are similar to those observed in another fishery known to be over-exploited, then by analogy the fishery of interest may also be in need of regulation. Symptoms of overexploitation have been described for populations of teleosts by the Strategic Planning for Ontario Fisheries (SPOF) Working Group (1983) but a comparable list for elasmobranchs has yet to be developed. Such a list would probably rely heavily on changes in baseline (preferably pre-exploitation) life-history parameter values. Signs of overexploitation might include increase in growth rates and fecundity, reduction in mean age and mean size in the population, reduction in age at maturity, reduction in the proportion of females that are gravid or carrying sperm in the oviducal gland, etc.

Life-history studies can provide massive amounts of information with potential uses in a number of disciplines. The questions then become "How can we assimilate and synthesize this information?" and "Is there any logical framework for explaining the observed variability in life-history parameters?" From a practical point of view, such a framework is needed to suggest comparative studies that might result in useful methods for estimating parameters, to provide guidance in determining what parameters may be useful in identifying overexploitation, and for developing methods to rank species according to their resilience to exploitation. We believe that r/K selection theory is useful for these purposes.

r/K Selection Theory

The theory of r/K selection has been around for quite awhile (MacArthur and Wilson 1967) and it has its share of adherents and critics. It is intimately related to the logistic model of population growth (whose parameters are " r " and " K "), and the logistic model provides the theoretical basis for the stock production model of Schaefer (1957). It is thus of interest to study the connections between r/K selection theory and fisheries management models.

Let us begin with a consideration of the logistic model of population growth. Though the logistic curve dates back to Verhulst in the early nineteenth century, modern interest in the logistic model can be traced to Lotka's (1925) work on human populations and to Volterra's (1928) work on fish. Imagine an undisturbed population inhabiting a constant environment for a long period of time. The population has reached an equilibrium state so that the number

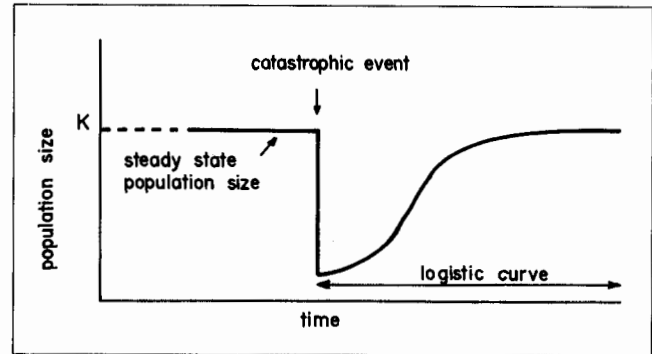


Figure 2.

Representation of population size of a hypothetical population over time. Population begins at equilibrium at the carrying capacity of the environment, undergoes a catastrophic decline, and recovers according to the logistic model of population growth. K is the maximum (asymptotic) size of the population.

of births exactly balances the number of deaths and the number of animals present remains constant (Fig. 2). Now suppose that some kind of catastrophic event occurs and the population is suddenly reduced. One would expect that there must be some way for the population to recover, otherwise every successive catastrophic event would push the population closer to extinction. With reduced numbers present, more resources become available for each individual so the survival rate might increase. With more energy available, the organisms should be able to devote more effort to growth and reproduction. Thus, we might see an s-shaped recovery curve for population size as a function of time. This is the logistic model which says, in essence, that in a salubrious and uncrowded environment, where there are no resource limitations, the population growth trajectory may approach an exponential curve, but as the population increases resources again become limiting and the population growth approaches zero. Mathematically, the rate of population increase, dN_t/dt , can be described by

$$dN_t/dt = r N_t (K - N_t)/K, \quad (2)$$

where N_t is the population size (in numbers or in biomass) at time t , K is the maximum (asymptotic) size of the population and is usually called the carrying capacity of the environment, and r is a scale parameter which controls how fast the population can increase. The parameter r is known as the intrinsic rate of population increase. Equation (2) describes the rate of growth at any particular population size. To determine the size of the population at any time we need to integrate Equation (2). Thus, the population size at time t is given by the s-shaped curve (Fig. 2)

$$N_t = K/(1 + b e^{-rt}), \quad (3)$$

where b is a location parameter which is related to the size of the population at time $t = 0$.

Note that when N_t is close to zero, the factor $(K - N_t)/K$ in Equation (2) is close to 1. So, the rate of change of the population at low population sizes is close to

$$dN_t/dt \approx r N_t. \quad (4)$$

Expressed in words, the rate of growth is proportional to the size of the population present and the growth over time is similar to the growth of money in a savings bank. More formally, the integrated form of (4) is given by the exponential curve

$$N_t = N_0 e^{rt}, \quad (5)$$

where N_0 is the initial size of the population (at $t = 0$).

Consider a species that lives in an unstable, unpredictable environment. Such a species suffers catastrophes often and must be biologically adapted to respond quickly to new, uncrowded conditions. Thus, it must have a high value of “ r .” In contrast, a species living in a very stable environment must be able to withstand competition and use its limited resources efficiently but need not necessarily be equipped to deal with sudden, dramatic shifts in environmental conditions. It must be adapted for conditions at or near the carrying capacity of the environment. We say that the former type of species is r -selected while the latter is K -selected.

The appeal of this concept is that it provides a framework for judging the evolutionary and survival values of life history traits. That is, we can predict that certain traits would tend to be found in r -selected species while others would be found in K -selected species. Ricklefs (1979) and others list the following characteristics:

r -selected traits	K -selected traits
chooses variable and/or unpredictable habitats	chooses constant and/or predictable habitats
frequently colonizes or recolonizes	rarely colonizes or recolonizes
niche broad	niche narrow
“small” body size	“large” body size
rapid development	slow development
high fecundity	low fecundity
early reproduction	delayed reproduction
semelparity	iteroparity
high and/or catastrophic mortality; density independent mortality	low and/or constant mortality; density dependent mortality
short longevity	long longevity
highly productive	highly efficient at producing biomass

To the list of K -selected traits can be added elaborate social structures and mating systems, parental care of young, and storage of energy.

Based on the description in the last section of common life-history features of sharks, it would appear that this group is extremely K -selected. If the r/K selection theory

holds up under scrutiny, then it is of interest to ask to what extent can the theory be refined. The following question arises: Can we rank species along an r - K continuum and would this ranking provide some indication of the relative abilities of the species to withstand exploitation?

The theory of r/K selection has received wide attention and there are a number of generalizations, including a stochastic version of the theory known as bet hedging and the formulation of another type of selection called α -selection (see Emlen 1973). The latter concept deals with the depression in the rate of population increase due to interaction with other species. A species is called α -selected if it has evolved mechanisms to avoid competitive inhibition.

There are also a number of criticisms of the overall theory. One criticism, that the r/K selection theory doesn't answer all questions, can be dismissed out of hand since, for our purposes, we only need a theory that will provide useful information or predictions for management. That this criticism has been raised at all may be attributed to the high hopes that were generated by the formulation of r/K selection theory.

A more serious criticism is that the theory doesn't always seem to apply. For example, sticklebacks (*Gasterosteus* spp.) have small body sizes, short life spans, and other characteristics normally associated with r -selection but also have low fecundity and parental care of the young which is associated with K -selection. Stearns (1977) analyzed 35 studies and found that 17 species did not fit the r/K selection scheme. Still, that a simple and rather intuitive theory worked in about half the cases argues that it is still worth considering.

Another criticism is that the theory hasn't been tested properly. It is easy to list traits that one imagines should be associated with r - or K -selection and then to list species which fall near one extreme or the other. Ricklefs (1979) argues that one should also determine whether the species presumed to be r -selected face greater environmental variability and have greater variability in numbers than those presumed to be K -selected.

Four counter-arguments can be made to the last criticism. First, might not the consistent co-occurrence of traits associated with each extreme be viewed as supportive of the theory? Ricklefs (1979) argues that many life-history traits are correlated with body size and that biophysical differences in scale, rather than evolutionary selection, may account for small animals having “ r -selected” traits relative to larger animals. This argument of scale would not apply within a narrow size range. Second, in some cases it can be proved mathematically that a trait will be selected for (or against) in an unstable environment. Third, Emlen (1973) argues that “Populations held by inclement weather or predation to levels well below their carrying capacities experience primarily r_0 -selection [i.e., r -selection]. . .”. Thus, according to this view, great variability in environment or population size is not necessary to validate the model. However, we run into a difficulty with the definition

of carrying capacity. Consider a hypothetical, stable population which experiences some predation as part of its normal course of events. Is this population at the carrying capacity of its environment or is it held at a lower level by predators? In other words, is the carrying capacity a natural level of population size or is it a concept that only applies to an animal completely divorced from its natural environment? We leave it to others to grapple with this question. The interested reader should consider studies by Pauly (1979) and Larkin and Gazey (1982). The fourth counter-argument to the criticism of lack of validation is that one can estimate the intrinsic rate of increase in some cases and thus we can see how r -selected are the species that we have presumed to be in this category.

Estimating the Rate of Population Increase

Estimating the Value of r from a Logistic Stock Production Model

The rate of growth of a population depends on the size of the population relative to the carrying capacity, as described by Equation (2). This curve is a dome-shaped, parabolic function of population size. Now, suppose the population is harvested at exactly the same rate at which the population is growing, i.e., at the rate dN/dt . Then harvest will just equal production and the population will maintain a steady state at the population size N . This level of harvest is known as "surplus production" because it can be continuously removed without lowering the population size. Thus, the sustainable yield is a parabolic function of population size. If one could observe the steady yields obtained at two or more points of time when the population

size is also known, then one could solve for (estimate) the parameters r and K . This is the basis of Graham's (1935) production model.

It is important to recognize that catch is not necessarily synonymous with production—they are synonymous only under equilibrium conditions. Thus, if 500 tons of biomass (say) are suddenly removed from an unexploited population, the population production will rise in response to the removal. But, the removal itself is not surplus production. If one treats all biomass removal as if it were removal of surplus production, one will tend to overestimate the value of the maximum sustainable yield. In a developing shark fishery, much of the harvesting may amount to simple biomass removal rather than removal of surplus production. This is particularly true if the fishery develops rapidly. Reduction of the population cannot continue indefinitely, or one will observe a "boom or bust" type fishery. This does not mean that a sustained harvest cannot be maintained at a sufficiently low level.

Although it is at least conceptually easy to measure the catch from a fishery, it is difficult to estimate population size. However, it is well known that sustainable yield under a logistic model is also given by

$$Y = K F - (K/r) F^2, \quad (6)$$

where F is the instantaneous rate of fishing mortality (see Ricker 1975, p. 315). Furthermore, fishing mortality is generally assumed to be proportional to fishing effort, i.e.,

$$q f = F, \quad (7)$$

where f is the fishing effort and q is known as the catchability coefficient. Therefore, sustainable yield is also a parabolic function of fishing effort (Schaefer 1957):

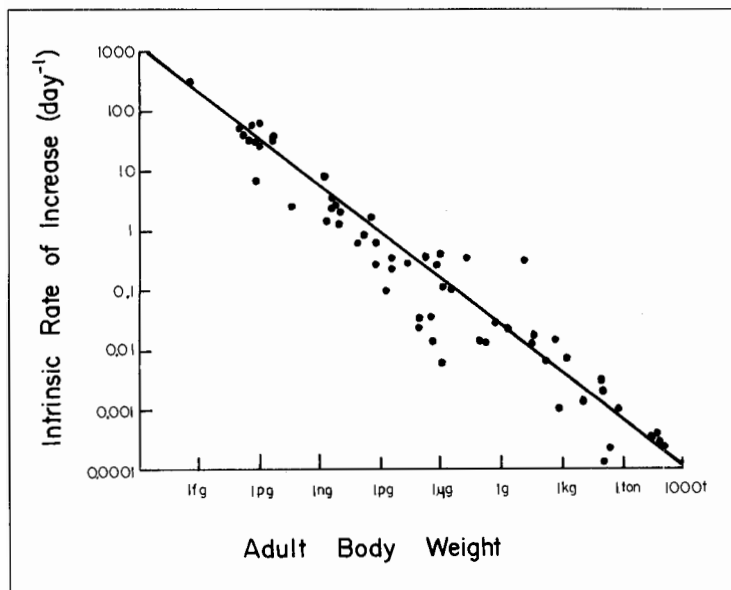


Figure 3.

Relationship between the estimated intrinsic rate of increase of various organisms and their adult body weight (modified from Blueweiss et al. 1978 by Pauly 1982).

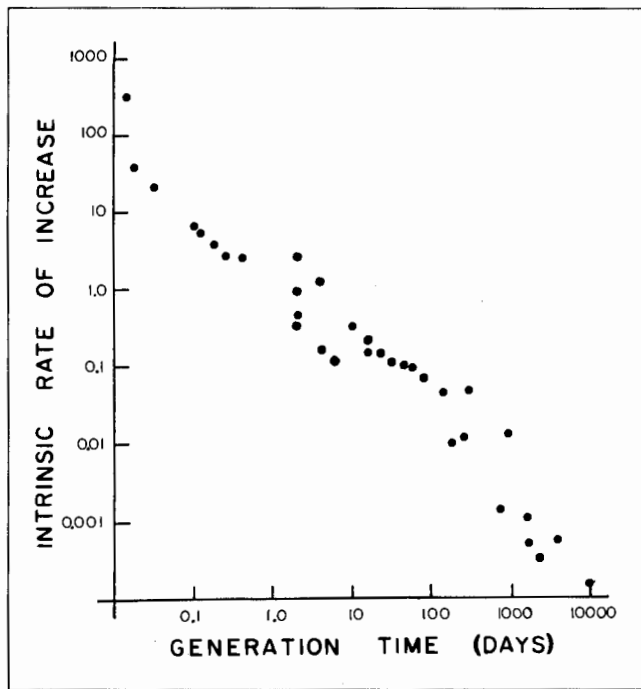


Figure 4.

Relationship between the estimated intrinsic rate of increase of various organisms and the generation time (modified from Heron 1972).

$$Y = (Kq)f - (Kq^2/r)f^2. \tag{8}$$

The stock production model can be fitted to observations on catches and the corresponding fishing mortalities (when conditions in the fishery are at equilibrium, i.e., stable) in order to obtain estimates of maximum sustainable yield, optimum fishing mortality, etc., as well as estimates of r and K . The model can also be fitted to observations on catch and effort (or catch rate and effort), but some additional information is needed to estimate q in order to obtain estimates of r and K .

Stock production data are notoriously variable and it is difficult to meet the equilibrium assumption of the model. A number of methods have been developed to deal with these problems (see, e.g., Gulland 1983; Schnute 1977). But, it is not clear whether a comparative study of estimates of r from production models would lead to useful generalizations though this was suggested by Caddy and Csirke (1983).

Comparative Studies of r

A number of estimates of intrinsic rate of increase, r , are available in the literature for organisms ranging in size from viruses to whales (24 orders of magnitude). Most estimates are based on laboratory studies. The intrinsic rate of in-

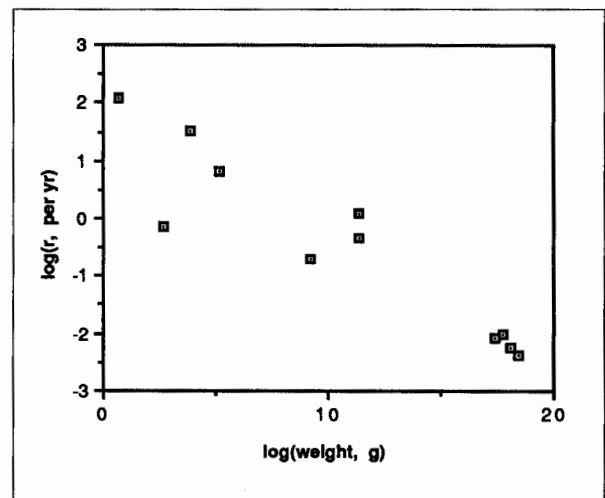


Figure 5.

Relationship between estimated intrinsic rate of increase of fishes and whales and their adult body weight. (Data from Pauly [1982] plus an additional case [courtesy of Alec MacCall, National Marine Fisheries Service, Tiburon, CA, personal communication, summer, 1983]: northern anchovy (*Engraulis mordax*) off California, $r = 0.88 \text{ yr}^{-1}$, $w = 15 \text{ g}$.)

crease appears strongly related to adult body size and to generation time (Figs. 3, 4). It is not clear how useful these relationships would be over a small portion of the range of the explanatory variable (body weight or generation time) though the relationship in Figure 5, dealing with fishes and whales, is encouraging. Indeed, Pauly (1982) suggested that the intrinsic rate of increase (per day) might be estimated, albeit crudely, from the regression model

$$r = 0.025 w^{-0.26}, \tag{9}$$

where w is defined to be the mean of the weight at first maturity and the maximum weight (both expressed in grams). Based on this, the maximum sustainable yield can be estimated as (Ricker 1975, p. 315)

$$\text{MSY} = rK/4. \tag{10}$$

“Book Keeping” Methods for Estimating Rate of Population Growth

It is also possible to estimate the observed (rather than the intrinsic) rate of population increase from schedules of age-specific survival and fertility. Either a life table or Leslie matrix model approach can be used. These methods essentially project a population forward in time and keep track of all survivors and offspring. We will consider the use of the Leslie model as described by Vaughan and Salla (1976).

Suppose we have data of the following sort:

Age, i	Survival, S_i	Female offspring, b_i
0	0.50	0
1	0.85	0
2	0.85	0
.	.	.
.	.	.
11	0.85	0
12	0.85	2.5
13	0.85	2.5
.	.	.
.	.	.
24	0.85	2.5
25	0	2.5

These data are based on the life history of the lemon shark, *N. brevirostris*. Based on tetracycline validated growth marks in vertebral centra, Brown (1988) reported the age at maturity for females to be approximately 13 years and the oldest age observed to be 21 years. Longevity is probably somewhat higher since the largest specimens examined were considerably smaller than the maximum reported size. A longevity of 26 years suggests, on the basis of a regression relating mortality to longevity (Hoenig 1983), that the annual survival rate is around 85%. Alternatively, an estimate of instantaneous natural mortality, M , can be obtained from Pauly's (1980) regression relating mortality to von Bertalanffy growth parameters and mean water temperature. Assuming a mean water temperature of 24°C (Gruber, unpubl. observations) and the von Bertalanffy parameter estimates in Brown (1988), one arrives at an estimate of M of 0.12 which corresponds to an annual survival of 89%. Litter size is around 8 to 12, of which half are females (Clark and von Schmidt 1965). Females in the related species (*Negaprion acutidens*) bear litters every other year (Stevens 1984) as apparently do females of *N. brevirostris*. Hence each female produces 2.5 females per year on average. Survival rate in the first year is estimated to be 50% (Gruber, unpubl. research).

Suppose further that the age composition in a certain year t is the following:

Age	Number at age
0	n_{0t}
1	n_{1t}
2	n_{2t}
.	.
.	.
25	n_{25t}

Then we can calculate the age composition in the next year, i.e., at time $t + 1$. The number of newborns will be the sum of the offspring produced by each age in year t :

$$n_{0,t+1} = \sum_{i=0}^{25} n_{it} b_i$$

$$= n_{0t} \cdot 0 + n_{1t} \cdot 0 + \dots + n_{25t} \cdot 2.5. \quad (11)$$

The number of one-year olds will be equal to the number of age-0 animals which survive to the next year:

$$n_{1,t+1} = n_{0t} \cdot s_0 = n_{0t} \cdot 0.5.$$

Similarly, the number at any age i (above age 0) in year $t + 1$ is given by

$$n_{i,t+1} = n_{i-1,t} \cdot s_{i-1}. \quad (12)$$

These relationships can be expressed compactly in matrix notation. Define the population projection matrix A to be

$$A = \begin{bmatrix} b_0 & b_1 & b_2 & \dots & b_{25} \\ s_0 & & & & \\ & s_1 & & & \\ & & s_2 & & 0 \\ & & & \ddots & \\ & 0 & & & s_{24} \end{bmatrix}. \quad (13)$$

(All elements of A are zero except the first row and the first subdiagonal.) Also, denote the population age structure at time t by

$$N_t = \begin{bmatrix} n_{0t} \\ n_{1t} \\ n_{2t} \\ \vdots \\ n_{25t} \end{bmatrix}. \quad (14)$$

Then the population at time $t + 1$ can be found by

$$N_{t+1} = A N_t. \quad (15)$$

The rate of population increase, $r(\text{obs})$, can be found from the largest eigenvalue (λ) of the matrix A by the relationship $r(\text{obs}) = \log_e(\lambda)$ (Vaughan and Saila 1976). However, Vaughan (1977) provided a more direct method for finding the rate of increase as the solution of the following equation:

$$\frac{e^{r(\text{obs})}}{S_0} = b_1 + \sum_{i=0}^I b_{i+1} e^{-i r(\text{obs})} \prod_{j=0}^i S_j, \quad (16)$$

where I is the oldest age class in the population (starting with age 0).

Since it may be difficult to interpret a value of $r(\text{obs})$, a convenient alternative is to compute the theoretical doubling time for the population. Under exponential growth, the population size at time t is

$$N_t = N_0 e^{r(\text{obs})t}$$

so

$$\frac{N_t}{N_0} = e^{r(\text{obs})t}.$$

Setting N_t/N_0 equal to 2 and solving for t gives

$$\text{time to double} = \frac{\log_e 2}{r(\text{obs})}. \quad (17)$$

This computed time-to-double will equal the actual doubling time if the population has a stable age distribution; otherwise, the computed doubling time may be larger or smaller than the actual doubling time. Nonetheless, Equation (17) provides a useful way to visualize the significance of a value of $r(\text{obs})$. Another possibility would be to compute the annual percentage change in population size under the same assumption of a stable age distribution.

Estimating age-specific fertility is generally feasible. Estimating survival rates is more difficult but can still be done. However, among teleosts, the first year survival rate is so highly variable and so difficult to measure, that estimates are of questionable use.

The elasmobranchs present a very different situation. The small numbers of well-developed young suggest that first year survival is stable and fairly similar to juvenile and adult survival. As a consequence of the elasmobranch life-history pattern, the Leslie model may prove useful for management of these fishes in three ways.

First, if all survival rates (including first year) are known, then the rate of population increase can be calculated using Equation (16) (Vaughan 1977). (Note that the rate of increase obtained in this way refers to growth in numbers rather than to growth in biomass.) Second, if all survival rates except that in the first year are known, and if the population is assumed to be at equilibrium, then first year survival can be calculated from Equation (16). One can thus study the effects of changes in parameters on the rate of increase and the first year survival rate. For example, one could calculate what would be the rate of increase if all young survived their first year of life or if first year survival equalled that of adults. In this way, one can explore the probable upper limits to the intrinsic rate of increase. Third, the Leslie matrix can be used to model the time to recovery of a depressed population. Schaaf et al. (1987) compared, for various species of teleosts, the time it takes to recover (to 80% of the initial abundance) following a one-time catastrophic reduction in survival of young-of-

the-year fish, e.g., as the consequence of a pollution incident. They assumed no compensatory mechanisms were operative. For elasmobranchs, studies can be directed towards determining the length of time to recovery for various species following cessation of fishing under a variety of scenarios of compensation. For example, one might assume that first year survival increases to the adult level, age of maturity is reduced by one or two years, fertility increases 25%, etc.

Consider the lemon shark data in the text table. The computed value of $r(\text{obs})$, based on these parameter values, is 0.015 yr^{-1} , corresponding to a doubling time of 46 yr (Table 1). Since lemon sharks are not believed to have been heavily exploited at the time these estimates of life-history parameters were made, the parameter estimates ought to imply a rate of increase close to zero (i.e., a large doubling time or, if the estimate is negative, a large halving time). This prediction is borne out by the assumed parameter values but this result may be fortuitous. A first-order sensitivity analysis suggests that $r(\text{obs})$ may be in the range -0.04 to 0.07 with a corresponding wide range of doubling times (lines 2 through 10, Table 1). Thus, it appears that apparently minor changes in parameter values can have significant effects on population dynamics. The results also suggest that it may be difficult to estimate life-history parameters with sufficient precision to understand the dynamics of a specific population.

If the lemon shark population is assumed to be at equilibrium ($r(\text{obs}) = 0.0$), then the first year survival rate would have to be 39% to balance Equation (16), given the parameter values in line 1 of Table 2. First-year survival rate computed under a variety of seemingly plausible scenarios ranges from 16 to 97% (Table 2). For example, if survival of all age groups (except the young of the year) decreases from 85% to 80%, then first year survival would have to rise to 96% to prevent a decline in population, all other things being constant.

Applications to Fisheries Management

The foregoing provides a number of ways in which the consideration of life-history patterns and r/K selection theory can provide guidance in the management of elasmobranch stocks. First, certain life-history parameters (natural mortality, growth, etc.) enter directly into fisheries assessment models. Estimation of population parameters is an inexact science, so it is important to assess the possibility of errors in the information available for assessment. A reasonable approach is to compare parameter estimates for one species with those for a similar species. This idea is easily generalized to enable one to consider patterns in parameter values among species. Indeed, some parameters appear to be so closely correlated that information on one easily estimated parameter can be used to estimate another, more difficult

Table 1.

Computation of population rate of increase, r (obs), and doubling time, $t(d)$, of lemon sharks (*N. brevirostris*) from a Leslie matrix model. The first line represents baseline conditions, i.e., computations based on best available information.

Assumed parameter values ^a					Computed results ^b			
$t(\text{mat})$	$t(\text{max})$	b	S	S_0	$r(\text{obs})$	% change	$t(d)$	% change
12	26	2.5	0.85	0.50	0.015	—	46	—
11	26	2.5	0.85	0.50	0.028	84	25	-46
13	26	2.5	0.85	0.50	0.004	-76	191	312
12	25	2.5	0.85	0.50	0.014	-6	49	7
12	27	2.5	0.85	0.50	0.016	5	44	-5
12	26	2.0	0.85	0.50	0.001	-93	624	1246
12	26	3.0	0.85	0.50	0.026	76	26	-43
12	26	2.5	0.80	0.50	-0.042	-380	-17	-136
12	26	2.5	0.90	0.50	0.068	358	10	-78
12	26	2.5	0.85	0.45	0.008	-44	83	78
12	26	2.5	0.85	0.55	0.021	40	33	-28

^a $t(\text{mat})$ = age of maturity; $t(\text{max})$ = maximum (truncated) age; b = number of females born per mature female per year; S = annual survival rate after the first year of life; S_0 = probability of surviving the first year of life.

^b $r(\text{obs})$ = observed or realized rate of population increase per year; $t(d)$ = theoretical doubling time in years corresponding to $r(\text{obs})$, assuming a stable age distribution. % change is the percentage change relative to base-line conditions.

Table 2.

Computation of first-year survival rate, S_0 , of lemon sharks (*N. brevirostris*) from a Leslie matrix model. The first line represents base-line conditions, i.e., computations based on best available information. Symbols are as defined in Table 1.

Assumed parameter values					Computed results	
$t(\text{mat})$	$t(\text{max})$	b	S	$r(\text{obs})$	S_0	% change
12	26	2.5	0.85	0	0.39	—
11	26	2.5	0.85	0	0.33	-16
13	26	2.5	0.85	0	0.47	20
12	25	2.5	0.85	0	0.40	2
12	27	2.5	0.85	0	0.39	-1
12	26	2.0	0.85	0	0.49	25
12	26	3.0	0.85	0	0.33	-17
12	26	2.5	0.80	0	0.97	146
12	26	2.5	0.90	0	0.16	-59

to estimate parameter. We have already considered the estimation of intrinsic rate of increase from adult weight and generation time (Figs. 3-5). Another example is the estimation of natural mortality rate from longevity (Fig. 6) or from von Bertalanffy growth parameters and water temperature (Pauly 1980). This approach is becoming increasingly popular (Adams 1980; Gunderson 1980; Myers and Doyle 1983; Gunderson and Dygert 1988). These comparative approaches are admittedly crude but they are surely better than nothing.

Because many elasmobranchs currently have a relatively low commercial value or are harvested by difficult to sample sport fisheries, it seems likely that assessment models

and regulations will have to be based on incomplete information. For this reason, we have explored a number of simple approaches for assessing stocks, such as monitoring changes in growth rates and other life-history parameters. This obviously requires good baseline data. We have hinted that it may be possible to develop criteria for ranking species according to their capacity to withstand exploitation. From r/K selection theory, we are led to believe that natural mortality rate, age at maturity, and fecundity may be useful for these purposes. The intrinsic rate of increase should be a most useful criterion for ranking species but this parameter is difficult to measure. Fortunately, intrinsic rate of increase and natural mortality appear to be closely related to other parameters such as growth and longevity so that there may be simple ways to obtain approximate values.

Monitoring stock abundance could provide useful management information for those species that can be effectively sampled. These might include species that have well defined nursery areas in bays and lagoons. However, many species have complicated, poorly understood distributional patterns which vary with sex, size, and season. Designing effective, fishery-independent sampling programs is likely to be exceedingly difficult for these species.

The Leslie matrix model (or similar age-structured model) appears to be a useful way to simulate elasmobranch populations. In the absence of sufficient fisheries data, biologists will probably have to settle for experiments with these simulated populations in order to develop management strategies. We have already shown how the Leslie model can be used to estimate survival in the first year of life and to place bounds on the probable value of the

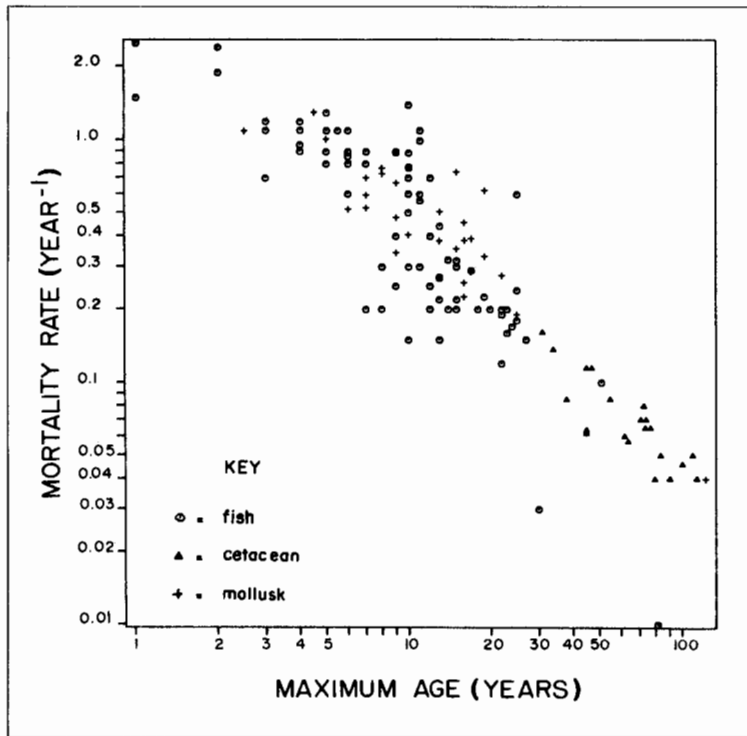


Figure 6. Relationship between the estimated instantaneous mortality rate and the maximum age known for 125 stocks of fish, mollusks, and cetaceans (from Hoenig 1983).

intrinsic rate of increase. It might also be used to determine how much fecundity/first year survival must change in order to compensate for an increase in adult mortality. Grant et al. (1979) suggested as a rule of thumb that harvest should be controlled so that the production of young did not fall below 50% of the unexploited level. They did not explore the consequences of this assumption in terms of required changes in life-history parameters. The model can also be used to study recovery times following a decrease in fishing mortality.

A number of workers have suggested that egg-per-recruit analysis is a useful tool for fishery management (e.g., Prager et al. 1987). This concept pertains to equilibrium situations and is difficult to interpret unless the egg-per-recruit is compared to the virgin (unexploited) level. Computation of egg production as a percentage of the virgin level is straight forward and can be applied to both equilibrium and nonequilibrium situations. It remains to be seen how well the 50% rule of Grant et al. (1979) works in practice.

The Leslie matrix model would be useful for evaluating the consequences of harvesting "surplus" males while protecting females. Many terrestrial big game populations are managed in this manner. Since the males of all elasmobranchs are readily identified by the presence of external claspers and many elasmobranchs segregate by size and sex, this approach may be feasible for many species, particularly for large sharks. The evaluation of such a management scheme should be based on monitoring the abundance

of juveniles or the frequency of occurrence of gravid females over time and, for those species which store sperm, the proportion of females retaining sperm in the oviducal gland. In theory, a differential harvest of the sexes could provide a sound basis for the application of change in ratio techniques for estimating population size and other parameters (Seber 1982). This would require accurate catch statistics and accurate fishery-independent assessments of sex ratios and thus does not appear to be a viable option for widespread use.

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